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Partial migration of a maraena whitefish *Coregonus maraena* population from the River Elbe, Germany

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ABSTRACT: The maraena whitefish *Coregonus maraena* is a threatened anadromous species in the North Sea, which in the past was decimated to near extinction. Since the late 1980s, several re-establishment programs have been implemented in rivers draining into the North Sea, but the scientific basis for sustainable conservation measures is often lacking, since little is known about the biology of this species. In this study, otolith microchemistry of fish ranging from 24.6 to 58.4 cm in total length (median 31.3 cm, SD 8.4 cm) was used to characterize the migration behavior of a reintroduced population of maraena whitefish from the River Elbe, Germany. Our analyses revealed the presence of 3 different migration patterns: (1) one-time migration into high-salinity habitat (North Sea) within the first year of life (29.6%), (2) multiple migrations between low- and high-salinity habitats starting in the first year of life (14.8%) and (3) permanent residency within low-salinity habitats, a pattern displayed by the majority (55.6%) of sampled individuals. Not only do these results reveal differential migration behavior, but they also indicate that permanent river residency is common in the River Elbe population of *C. maraena*. The role of the Elbe as both a feeding and a spawning habitat should thus be considered more explicitly in current conservation measures to support recovery of this species.

KEY WORDS: Migratory fish species · Conservation · Otolith microchemistry

1. INTRODUCTION

A major threat for diadromous fish species is habitat alteration, which includes physical and chemical barriers that block natural migration routes, but also causes the direct loss of freshwater habitat for spawning or nursery (de Groot 2002, Limburg & Waldman 2009). Furthermore, as most diadromous species are of commercial importance, fishing is a contributing factor to the decline of many species (Limburg & Waldman 2009). These threats apply to both anadromous species migrating into rivers to spawn (e.g. salmonids), and to catadromous species migrating into the sea to spawn (e.g. eels).

The maraena whitefish *Coregonus maraena* is a salmonid species (Salmonidae) and belongs to the subfamily Coregoninae (Nelson et al. 2016). The Coregoninae is a diverse taxon from the northern hemisphere, which demonstrates considerable variation both among and within species regarding morphology and behavior, for instance in the number of gill rakers or the migration strategy (e.g. Hansen et al. 1999, Harris et al. 2012, Jacobsen et al. 2012).

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In the majority of studies and in recent conservation efforts, the anadromous North Sea form of *C. maraena*, the subject of the present study, has been designated as North Sea houting *C. oxyrinchus*, e.g. in the Danish EU LIFE project running from 2005 to 2012 and the EU Habitats Directive (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora). However, the nomenclature within the genus *Coregonus* has led to considerable discussion and confusion. Since the consideration of houting in the North Sea is not limited to the possibly extinct species *C. oxyrinchus*, but rather to the North Sea population of *C. maraena* (Bloch 1779) or a previously undescribed species (Kottelat & Freyhof 2007), we use the scientific name *C. maraena* instead of *C. oxyrinchus* following Mehner et al. (2018). Whether whitefish populations from the North Sea should be considered a separate species from those in the Baltic Sea is still subject to scientific discussions (Dierking et al. 2014, L. F. Jensen et al. 2015, Mehner et al. 2018). However, there is evidence that the extant form of whitefish from the North Sea should be classified as a separate evolutionarily significant unit for conservation purposes, independent of the actual species status (Dierking et al. 2014).

In the North Sea, *C. maraena* was formerly common and widespread throughout the Wadden Sea region (Duncker & Ladiges 1960, Jensen et al. 2003). In the 20th century, anthropogenic activities such as river regulations including the building of dykes, groins and sluices, as well as pollution (Hansen et al. 1999, Kammerad 2001b, Jensen et al. 2003), caused migration barriers and habitat loss, including the deterioration or even elimination of spawning grounds (Grøn 1987, Kammerad 2001b) and consequently almost led to the extinction of *C. maraena* (Hansen et al. 1999, Jensen et al. 2003).

In the River Elbe drainage system, which includes one of the largest European estuaries (Pihl et al. 2002), *C. maraena* fisheries with annual yields of up to 23 t were supported until the early 20th century (Kammerad 2001a,b), but then the population collapsed due to reasons mentioned above and this species became locally extirpated. Similarly, other anadromous species have been negatively affected (e.g. Atlantic salmon *Salmo salar*, twaite shad *Alosa fallax*, river lamprey *Lampetra fluviatilis*) or have been locally extirpated, e.g. sturgeon *Acipenser sturio* and allis shad *Alosa alosa* (Thiel & Thiel 2015). In the North Sea, only 2 small remnant populations of *C. maraena* persisted in the Danish rivers Vidå and Ribe Å (Jensen et al. 2003).

Currently, *C. maraena* is classified as 'Vulnerable' (VU A2cd) in the IUCN Red List (Freyhof 2011), and as 'threatened' and/or 'declining' by the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Convention), and it is a priority species listed in Annexes II and IV of the Habitats Directive. This means that special areas of conservation are required for the conservation of the species, and the species is in need of strict protection (Svendsen et al. 2018).

The first programs for re-establishment of *C. maraena* in formerly inhabited rivers in the North Sea were set up for several Danish rivers and the German Eider–Treene river system in the late 1980s (Kammerad 2001b, Jensen et al. 2003, Jepsen et al. 2012), followed by the Rivers Elbe and Rhine (Kammerad 2001b, Borcherding et al. 2010, Dierking et al. 2014). Since 1997, the Elbe tributaries Seeve, Este, Oste, Luhe and Aue (Lühe) have each been stocked annually with 10 000–15 000 fingerlings of *C. maraena* (2–3 cm long) in spring, i.e. a few weeks after hatching in April (see www.schnaepel.de/). Nevertheless, natural reproduction in the River Elbe in the recent past has occurred only on a very low level (Thiel & Thiel 2015). To date, these programs have relied heavily on stocking, as currently too little is known about the environmental improvements needed for a natural recovery of these populations (Svendsen et al. 2018). At present, habitat conditions generally considered important for diadromous species, such as water quality and passability, have improved in several rivers (de Groot & Nijssen 1997, Borcherding et al. 2010), in principle paving a possible path to recovery in the future.

Investigations of *C. maraena* in the River Vidå showed that adult fish entered the river mostly in October and arrived at putative spawning areas in November (Hertz et al. 2019). Downstream migration started predominantly in December, and the fish entered the Wadden Sea in March and April (Jensen et al. 2018). Other studies confirm spawning migrations into the rivers in early winter (Jepsen et al. 2012) and a return to the sea in spring (Jensen et al. 2003). However, other studies suggest a certain degree of intraspecific flexibility, both in terms of onset of migration and time spent in the river after spawning (Jensen et al. 2018) as well as in terms of dispersal migration behavior, including non-migrating individuals and migrations at larger size and higher age (Borcherding et al. 2008). To date, no studies on the migration behavior of *C. maraena* have been carried out in the Elbe.

Otolith microchemistry has become an important tool for the identification of migratory behavior, par-

ticularly for diadromous species (Walther & Limburg 2012). The concentration of strontium (Sr) and barium (Ba) in ambient water, given as element:calcium (Ca) ratios, varies with water salinity; the Sr:Ca ratio is generally positively correlated and the Ba:Ca ratio is generally negatively correlated with increasing salinity (Tabouret et al. 2010). Accordingly, Sr:Ca ratios are usually negatively correlated to Ba:Ca ratios. These elements are incorporated into the calcium carbonate matrix of hard structures such as otoliths by substituting for calcium (Kalish 1990). As otoliths are chemically inert (Campana & Neilson 1985), different concentrations of Sr and Ba in fresh- and saltwater are reflected in the chemical composition of all otolith growth zones just like spatial fingerprints. Element:Ca ratios measured along a transect from the nucleus-area to the edge of an otolith are therefore a suitable measure to reveal the migration history of diadromous fishes.

This study had the overarching goal to help close the knowledge gap with respect to habitat use and migration behavior of the *C. maraena* population in the River Elbe–Wadden Sea system. Specifically, our aims were (1) to characterize the use of low- versus high-salinity habitats (and thus migrations between the 2 habitats) of individuals from this population, (2) to assess the possible presence and prevalence of differences in migration behavior among individuals, and (3) to assess the role of possible underlying factors affecting migration behavior, such as ontogenetic changes and sex-specific differences. From an applied conservation perspective, this information can help resource managers to understand habitat requirements of this threatened species in the River Elbe–Wadden Sea system.

2. MATERIALS AND METHODS

2.1. Study area

The study area was located in the lower River Elbe between Hamburg and Cuxhaven in northern Germany (Fig. 1). The river section between Geesthacht and Cuxhaven, where the Elbe discharges into the North Sea, is tidal and exhibits a salinity gradient, ranging from almost 0 to around 32 PSU (Boehlich & Strotmann 2008). Fishes from this lower section can freely migrate between freshwater and saltwater as there is no migration barrier.

2.2. Sampling and otolith preparation

We obtained 27 adult/subadult specimens of *Coregonus maraena* from bycatch of professional fisheries in the lower Elbe in June/July 2012 and February/March 2013. Nine and 17 individuals were collected at 2 catch locations (Sites 1 and 2, respectively) in the freshwater section close to Hamburg, and 1 individual was caught in the polyhaline section (Site 3) of the Elbe close to Cuxhaven (Fig. 1). All fish were frozen after capture. One additional individual that was hatched and raised in a freshwater aquaculture farm

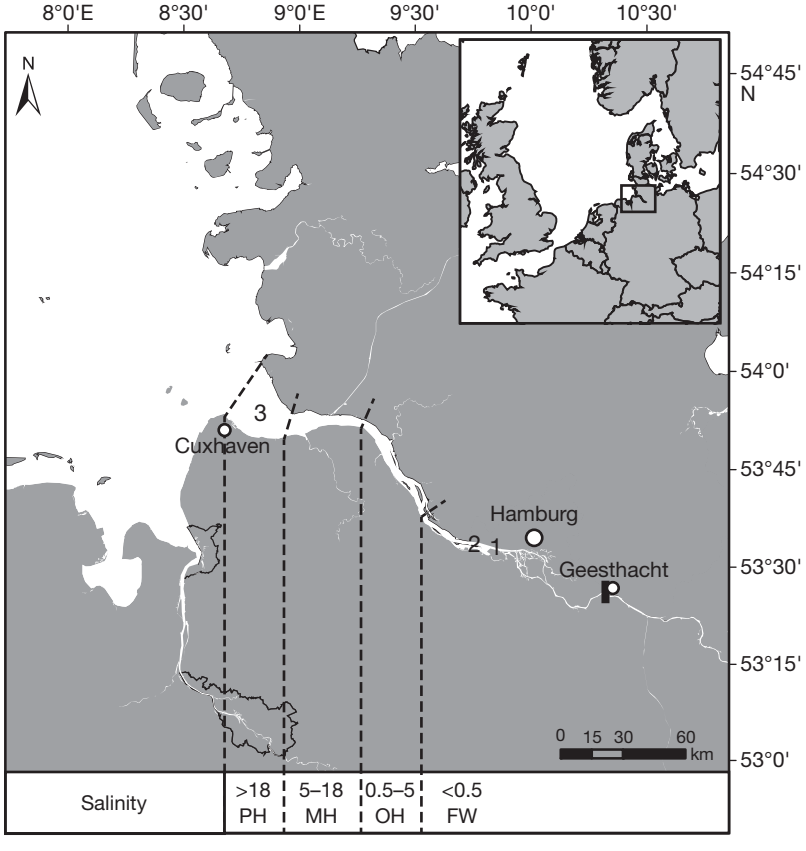

Fig. 1. Study area, showing the North Sea and the Elbe estuary in the German Bight. Freshwater (FW), oligohaline (OH), mesohaline (MH) and polyhaline (PH) sections of the estuary are shown (Stiller 2010). Sampling locations were in the freshwater section close to Hamburg, where 9 (Site 1) and 17 (Site 2) *Coregonus maraena* individuals were caught. One fish was caught in the polyhaline section of the River Elbe close to Cuxhaven (Site 3). The black bar marks the only migration barrier (weir) in the Elbe estuary

(BiMES Binnenfischerei, Leezen, Germany), and therefore experienced exclusively pure freshwater conditions over its lifetime, was obtained in July 2013 and served as a control.

After defrosting, total length (TL) and sex of the individuals were determined. Opercula were removed for subsequent age determination. Sagittal otoliths of all individuals were extracted, cleaned with distilled water and air dried. One randomly chosen otolith per individual was used for otolith microchemical analyses. Specifically, thin sections (0.5 mm) of the otoliths were cut and glued to glass slides with Crystalbond Mounting Wax (Buehler; http://www.buehler.com). These sections were then ground manually using lapping papers of 30, 12 and 3 µm, consecutively, until the core area could be detected under a light microscope (Leica DM 750). Finally, otoliths were polished using aluminum paste (ALPHA MICROPOLISH 2, grain size 0.3 µm).

2.3. Laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) analysis of otoliths

Microchemical analyses of otoliths were performed at the Department of Geosciences of Bremen University, Germany, using a NewWave UP193ss solid-state laser with 193 nm wavelength coupled to a Thermo Element2 ICP mass spectrometer.

Transects were set from the nucleus-area to the edge of each otolith. Like some other salmonids (Kalish 1990), *C. maraena* possesses not just 1 but 2 core areas in its otoliths. The midpoint between these 2 areas was defined as the nucleus of the otolith and set as the starting point of ablation (Fig. 2). Prior to ablation, the blank signal was recorded for 20 s.

The sample surface was pre-ablated with a spot-size of 75 µm and a scan speed of 100 µm s^{-1}. For transect ablation, a 50 µm spot-size with 3 µm s^{-1} scan speed and a laser pulse rate of 10 Hz was used. Irradiance was approximately 1 GW cm^{-1}. Flow rates of the carrier gas (helium) and the make-up gas (argon) were about 0.7 and 0.9 l min^{-1}, respectively. The intensities of the isotopes ^{88}Sr, ^{43}Ca and ^{143}Ba were measured. A synthetic glass (NIST 610; National Institute of Standards and Technology, Gaithersburg, MD) was used as an external calibration standard and was analyzed after every second transect. A correction for the isobaric interference of double-charged ^{86}Sr on ^{43}Ca was performed based on analyses of the carbonate reference standard MACS-3 (Jochum et al. 2012). Analytical precision and accuracy were assessed by analyzing a pressed pellet of the otolith reference standard NIES CRM No.22 (Yoshinaga et al. 2000) on each measurement day. Precision was around 5% and accuracy was better than 10%.

As a result of the automated sawing during the otolith preparation process, some otoliths were not perfectly cut in their core region. Thus, the first 150 µm of each measured otolith transect was excluded from subsequent analysis.

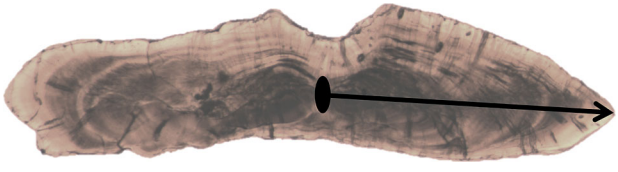

Fig. 2. Thin section of a *Coregonus maraena* otolith illustrating 2 core areas and the midpoint (black ellipse) defined as the otolith core from which transects (black arrow) were ablated

2.4. Differentiation between habitats

Different salinity regimes were identified from the frequency distribution of all Sr:Ca ratios measured using an approach similar to that of Daverat et al. (2011) and Magath et al. (2013). This approach is theoretically based on the expected multimodality of the frequency because *C. maraena* mainly uses 2 habitats of very different salinity (Wadden Sea as feeding habitat and freshwater for spawning and early life stages, e.g. Jensen et al. 2003). In a first step, a multimodal frequency distribution was plotted with singly measured Sr:Ca ratios of all individuals available. This distribution revealed 1 strong maximum at low Sr:Ca ratios and 2 weak maxima at higher Sr:Ca ratios. In the second step, the first strong maximum was separated from the 2 following weak maxima according to the expected main habitats in freshwater and Wadden Sea, which resulted in the assignment of a low-salinity (Sr:Ca ratios ≤0–2.1 mmol mol^{-1}) and a high-salinity regime (Sr:Ca ratios >2.1 mmol mol^{-1}, Fig. 3).

The established salinity regimes agree well with findings of the closely related *C. lavaretus* from the Baltic Sea, where sea-spawning individuals had Sr:Ca values >2.0 mmol mol^{-1} (Rohtla et al. 2017). Nevertheless, to further validate the approach, we used Sr:Ca ratios of fish from known salinity origins as reference. The freshwater reference was given by both the Sr:Ca ratios (all measurements) of the freshwater-reared individual which did not originate from the Elbe estuary ('freshwater control') and the last section (last 6 Sr:Ca measurements) of ablated transects of 26 individuals caught in the freshwater part

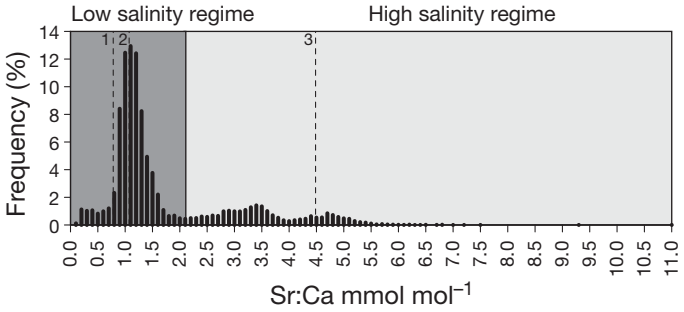

Fig. 3. Frequency distribution of all *Coregonus maraena* otolith Sr:Ca ratios, showing a low-salinity regime (limnic to slightly brackish water) and a high-salinity regime (medium brackish to euhaline water); numbers refer to reference material, where 1: 'freshwater control,' 0.78 mmol mol^{-1}; 2 'freshwater-caught fish,' 1.07 mmol mol^{-1}; and 3: 'polyhaline water-caught fish,' 4.48 mmol mol^{-1}

of the Elbe estuary, 'freshwater-caught fish', see Fig. 1). Similarly, the last 6 Sr:Ca measurements of the ablated transect of the 1 individual caught in the lower reaches of the Elbe estuary (i.e. in polyhaline waters at the time of capture, 'polyhaline water-caught fish', see Fig. 1) provided the reference values for habitat of higher salinity.

The calculated mean (±SD) value for freshwater-caught fish (Sr:Ca = 1.07 ± 0.44 mmol mol^{-1}) was slightly above the mean value of the freshwater control (0.78 ± 0.07 mmol mol^{-1}) and nearly equaled the strong first peak of the frequency distribution (Fig. 3), indicating that the defined low-salinity regime reflects limnic to slightly brackish waters. In contrast, the average Sr:Ca ratio of the polyhaline water-caught fish (4.48 ± 1.03 mmol mol^{-1}) was close to the third peak, thus the high-salinity regime likely reflected medium brackish to euhaline waters.

An inverse relationship between Sr:Ca and Ba:Ca ratios in the otoliths was observed (rho = −0.265, $p < 0.001$), which is well-known from studies on habitat use of migratory fishes along a salinity gradient (Walther et al. 2011).

2.5. Determination of age and annuli

For age determination, annuli were counted along each ablated otolith transect from the LA-ICP-MS analysis. For this purpose, these sections were viewed under a light microscope (Leica DM 750) at 40–100× magnification using transmitted light, and possible ring structures were examined. The results were verified by examining opercula, as annuli can be identified more precisely in these hard structures compared to otoliths (Gerson 2013).

2.6. Data analysis and statistics

Temporal habitat use and potential movements of fish between the specified habitats (low- and high-salinity regimes) were detected by measured Sr:Ca ratios along the ablation transects. Combined with age chronologies along the transects, this allowed for the reconstruction of individual migration life histories. Specific habitat uses and movements determined in this way were grouped into categories based on similarity (hereafter referred to as 'migration patterns'). Potential differences in the prevalence of these patterns between sexes and with age were then assessed using Fisher's exact test. Shapiro-Wilk tests were performed to test for normality of data. Because all data were not normally distributed, group sizes were unequal and sample size of subsets was small (<9), non-parametric tests were used for further comparisons (e.g. Raine et al. 2020). Correlations between Sr:Ca and Ba:Ca ratios as well as age and TL were tested using Spearman's rho statistic. Comparisons of fish size among sexes, age groups and migration strategies were conducted using the Mann-Whitney *U*-test. All statistical analyses were performed using R version 3.4.0 (R Core Team 2017).

3. RESULTS

3.1. Migration patterns

The otolith analyses revealed variability in migration behavior of maraena whitefish. Individuals either showed temporal habitat use and movements between the specified habitats (low-salinity regime including freshwater and slightly brackish water habitats and high-salinity regime including medium brackish to euhaline waters) or stayed permanently within the low-salinity regime. The signal profiles resulting from Sr:Ca measurements along the ablation transects were categorized into 3 patterns, as follows.

Pattern 1 was characterized by a one-time temporary increase in Sr:Ca ratios above the threshold of 2.1 mmol mol^{-1}. Eight individuals (29.6%) were assigned to this pattern. Of these, 7 showed a subsequent decrease in Sr:Ca ratios below the threshold along the transect (Fig. 4a), indicating one migration from a low- to a high-salinity regime, followed by a return into the low-salinity environment. Three individuals showed slight modifications of the underlying signal profile, with 2 individuals (Nos. 2 and 7 in Fig. S1 in the Supplement at www.int-res.com/articles/

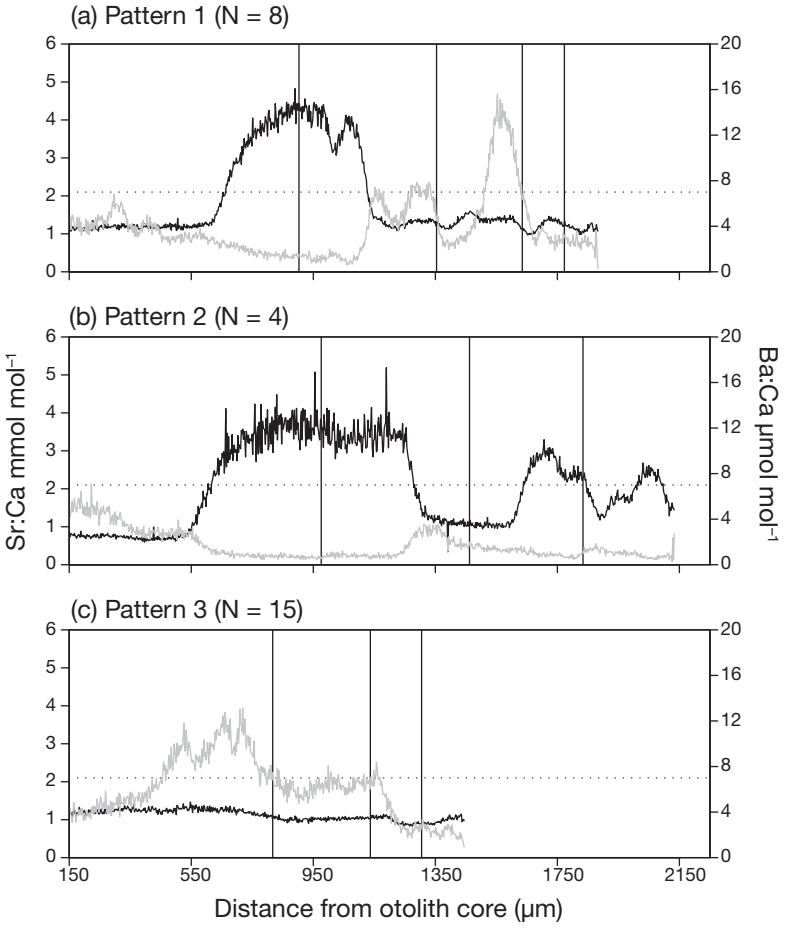

Fig. 4. Exemplary profiles of Sr:Ca ratio (black) and Ba:Ca ratio (gray) measurements along *Coregonus maraena* otolith transects illustrating (a) one-time migration into the high-salinity regime (pattern 1), (b) multiple migrations into the high-salinity regime (pattern 2) and (c) residency within the low salinity habitat (pattern 3). The dashed horizontal line marks the Sr:Ca threshold between the low- and high-salinity regimes. Vertical lines correspond to annuli

suppl/n044p263_supp.pdf) that already showed high Sr:Ca ratios at the beginning of the measurements, and 1 individual (No. 8 in Fig. S1) for which Sr:Ca ratios remained high and did not decrease to low-salinity values again. Median age of individuals exhibiting pattern 1 was 2 yr, with an age span of 1–4 yr. There was a strong correlation between Sr:Ca and Ba:Ca ratios (rho = –0.745, $p < 0.001$) of all associated individuals, indicating an inverse relationship.

Pattern 2 was characterized by repeated increases in Sr:Ca ratios above the predefined threshold along the transect (Fig. 4b), indicating several migrations between the 2 environments. Four individuals (14.8%) represented this pattern, with a median age of 3 yr (range 3–7 yr). An inverse relationship between Sr:Ca and Ba:Ca ratios was also detected here (rho = –0.638, $p < 0.001$).

For those fish that were assigned to pattern 1 or 2 and which thus showed at least 1 seaward migration, this behavior occurred early in life (at the age of 0+).

Pattern 3 was defined as a long-term stay, i.e. residency, in the low-salinity regime with no habitat change, and was characterized by a signal curve that remained constantly below the predefined threshold (Fig. 4c). The majority of fish (15/27; 55.6%) displayed this pattern, all of which were sampled in the freshwater section close to Hamburg (see Fig. 1, Sites 1 and 2). Median age of individuals was 2 yr (range 1–8 yr). Unlike in patterns 1 and 2, the value of the correlation coefficient (rho = 0.520, $p < 0.001$) indicated a positive correlation between Sr:Ca and Ba:Ca signal profiles.

3.2. Migratory behavior and sex

There was no significant difference between males and females in the relative proportions of migratory (pattern 1 or 2) versus resident (pattern 3) migration strategies, with 7 out of 15 assessed females (47%) and 5 out of 12 males (42%) representing the migratory strategy (Fisher's exact test, $p > 0.05$).

3.3. Migratory behavior and fish size

As expected, TL was highly positively correlated with age (Spearman's rho = 0.69, $p < 0.001$), so to detect differences in body length between migrating (patterns 1 and 2) and non-migrating (pattern 3) individuals, age needed to be considered. As the majority of individuals had an age of 2 or 3 yr (N = 22), the subsequent analyses considered only these 2 age groups (AGs). There was no significant difference in the TL between sexes for either AG 2 or AG 3, ($U = 34$, $p > 0.05$ for AG 2, $U = 5$, $p > 0.05$ for AG 3), so males and females were combined. For AG 2, migrating individuals showed significantly higher TL than resident individuals ($U = 7$, $p < 0.05$) with a median length of 38.1 cm (range 28.9–40.8 cm) compared to 28.8 cm (range 25.2–31.9 cm) in resident fish (Fig. 5).

For AG 3, there was also a trend towards higher body size in migrating individuals (median 37.2 cm, range 37.0–41.6 cm) compared to residents (median 32.3 cm, range 30.9–44.2 cm, Fig. 5), but this difference was not statistically significant ($U = 3$, $p > 0.05$).

4. DISCUSSION

After maraena whitefish had almost disappeared from the North Sea as a result of human disturbance, re-introduction programs have aimed to ensure the return of this fish species to its formerly native range including the River Elbe, and ultimately to the establishment of self-sustaining (i.e. supported by natural reproduction) populations. To date, however, these programs have relied on continuous restocking, as appropriate management measures supporting natural population replenishment are still lacking due to the poor knowledge of the biology of this endangered species (Svendsen et al. 2018).

The present study addressed this issue by investigating the habitat use and migration behavior of the reintroduced population of maraena whitefish in the Elbe for the first time. Using otolith microchemistry, 2 fundamentally different migration strategies were found and expressed among individuals ranging from 24.6 to 58.4 cm in TL (median 31.3 cm, SD 8.4 cm) and an age of 1 to 8 yr in this population: migration between different salinity regimes or permanent residency in low salinity habitat. This phenomenon, which is known as partial migration of a population (Chapman et al. 2012b), can offer advantages in terms of adaptation to variable environmental conditions, but it also has specific conservation implications, which are discussed further in Section 4.5.

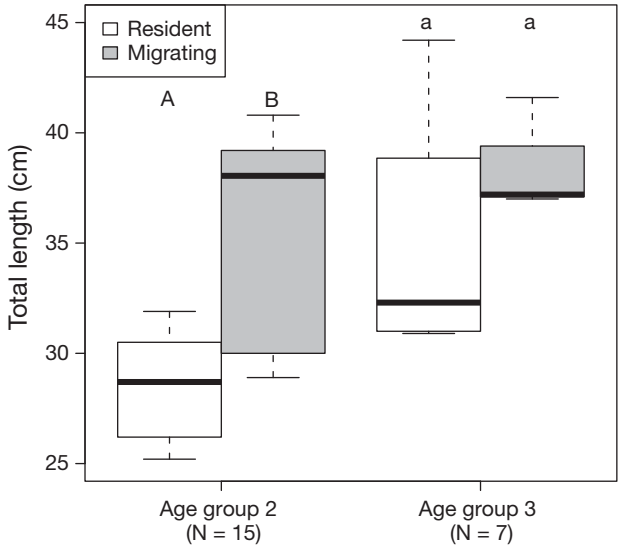

Fig. 5. Comparison of the total length of resident and migrating maraena whitefish of age group (AG) 2 and AG 3. Boxes represent the first and third quartiles, the horizontal line indicates the median, and whiskers extend to the most extreme data points. Within AGs, different letters above the plots indicate significant differences (Mann-Whitney *U*-test $p < 0.05$)

4.1. Migratory patterns

The finding of differential migration strategies, with 44% of the population showing migratory and 56% exhibiting permanent resident behavior, indicates a high degree of intraspecific variation within the Elbe population of maraena whitefish.

According to Jensen et al. (2003), maraena whitefish from the North Sea reach sexual maturity at the age of 2–3 yr (male) or 3–4 yr (female). Applied to this study, most sampled fish that showed permanent resident behavior were likely to be mature already (66.67%). The mean TL of those resident fish was 32.3 cm, ranging from 25.2 to 58.4 cm, and ages ranged from 1 to 8 yr. Borcherding et al. (2008) observed the migration behavior of maraena whitefish from the River Rhine and found that some of the sampled fish stayed in freshwater for a relatively long time and migrated when they had reached a TL of about 30–35 cm. Therefore, it cannot be excluded that several of the 15 individuals that presented pattern 3 in the present study (of which 7 were smaller than 30 cm) would also have migrated at a later point in time if they had reached a greater body length. However, a larger proportion already migrated in the juvenile stage at a TL of 35–40 mm. L. F. Jensen et al. (2015) also discussed an observation of an earlier study that also showed that juvenile *Coregonus maraena* of such a small size are already present in saltwater and even actively ingest food there, which indicates improved hyperosmotic tolerance in that early stage of life. In line with this, L. F. Jensen et al. (2015) compared the salinity tolerance of larvae and juvenile *C. maraena* and found that hyperosmotic tolerance increased with increasing body length. The juvenile *C. maraena* used in their study had a TL of 33–50 mm, indicating that those small fish develop the ability to hypo-osmoregulate and could migrate to higher salinities. In this context, it can be assumed that the non-migrating individuals in our study had already reached a tolerable size for migration long ago; and yet they did not do so.

This confirms earlier reports showing that populations of migratory fishes can have high migratory plasticity (e.g. Cucherousset et al. 2005, Miller et al. 2010, Magath et al. 2013), some including resident individuals (e.g. Jonsson & Jonsson 1993, Chapman et al. 2012b, Kendall et al. 2015). The partial migration of *C. maraena* shown here is also known from other coregonids in the northern hemisphere, e.g. *C. nasus*, *C. clupeaformis*, *C. sardinella* and *Stenodus leucichthys* (Tallman et al. 2002, Howland et al. 2009, Harris et al. 2012). Partial migration to brackish water has also been documented in Baltic Sea populations of European whitefish *C. lavaretus*, with some populations migrating to spawn in coastal rivers and streams, and others spawning in shallow, low-salinity bays in the northern Baltic Sea (Sõrmus & Turovski 2003). Moreover, the population from the River Tornionjoki (northern Baltic Sea) shows differential migration behavior in the marine phase, with part of the population staying in the northern Baltic and another part migrating further south to higher-salinity waters (Jokikokko et al. 2018).

Similarly to this study, migratory plasticity was also found in the *C. maraena* population from the Danish River Vidå (Jensen et al. 2018), but here migration behavior mainly differed between relatively large early- and late-migrating individuals (mean ± SD length 42.7 ± 6.4 cm) and was not characterized by a high degree of residency as identified in the present study. Although in the River Rhine, the majority of analyzed *C. maraena* were non-migrating (Borcherding et al. 2008), the situation was different from that in the Elbe, as migration barriers (large dams) in the Rhine delta possibly affected the natural migration behavior of *C. maraena*. In contrast, the high proportion of permanent residency in the Elbe, despite the absence of migration barriers, was exceptional and unexpected in the present study.

The development of a non-migrating tendency within an anadromous species may result from several and complex reasons (reviewed by Chapman et al. 2012a) that need to be considered in the context of the complete riverine and estuarine ecosystem. Gross (1987) argued that an anadromous lifestyle is useful when the benefits of more nutritious food in the marine habitat can offset the costs of a long migration into that habitat. Migration behavior reflects a balance between the benefits and cost of migrations that affects the fitness of fish (Jonsson & Jonsson 1993). The high proportion of permanent residency (i.e. feeding and spawning in the same habitat) in the Elbe in the present study would thus point to comparable net benefits for *C. maraena*.

In principle, migrations may be motivated by the need to spawn, feed and seek refuge from predators, but human activities may also influence the dynamics of fish migration (Chapman et al. 2012b). In the case of *C. maraena*, migration to feed in the sea but return to spawn is most likely, based on what is known about the life history of the species (Jensen et al. 2018). However, as the number of spawning individuals was not investigated, it is not possible to say conclusively whether or how many spawning migrations were carried out here.

The underlying data suggest that the reasons for migration were already effective very early in life. Specifically, if an individual did not leave the low-salinity environment in the first year of life, it also did not do so at a later point in time. In contrast, some individuals migrated during the first year of life, returned into the low-salinity environment and became resident thereafter (pattern 1). With a medium age of 2 yr, these individuals were relatively young. Therefore, it is possible that some of them would have migrated again later; also indicated by pattern 2, which is characterized by multiple migrations and older individuals (median age 3 yr but including 1 individual of 7 yr) than in pattern 1. Some of them returned to low-salinity environment in the same year of their hatch. This is well before they reach sexual maturity, reported at the age of 2–3 yr (males) or 3–4 yr (females) (Jensen et al. 2003).

In these cases, the migration thus does not represent a spawning migration. Immature maraena whitefish have been monitored in the lower sections of Danish rivers during winter (Jensen et al. 2003). This has also been observed in mature and immature individuals of closely related anadromous salmonids, especially within the genus *Salvelinus*, such as Arctic charr *Salvelinus alpinus*, which can return to rivers to overwinter (e.g. Klemetsen et al. 2003, A. J. Jensen et al. 2015). Similar behavior could also be a possible explanation for the early return of the fish examined here. The fact that the individuals assigned to patterns 1 and 2 were already caught in the Elbe in June/July also raises questions regarding contrasting temporal regulation of migration behavior among river systems, since spawning migrations have been observed in late fall in the Rivers Rhine (Borcherding et al. 2014) and Vidå (Hertz et al. 2019).

These observations suggest that living (including feeding) conditions in the Elbe may have been sufficient for *C. maraena*, possibly because of the low population density favoring residency (Jonsson & Jonsson 1993). The high residency rate also demon-

strates that the river system of the Elbe is likely to be of major importance for *C. maraena* not only as spawning but also as feeding habitat.

So far, it is unknown whether the reasons for the observed partial migration have an underlying phenotypic or genotypic origin. There is evidence that different genotypes as well as hybridizations of coregonids (*C. maraena* and non-migratory lake whitefish *C. lavaretus*) coexist in the Elbe (Dierking et al. 2014). *C. maraena* physiologically differs from *C. lavaretus* in terms of osmoregulation (Hertz et al. 2019). This is reflected in the ability of *C. maraena* to tolerate high salinities and undertake migrations into the North Sea, which *C. lavaretus* is not able to do (Grøn 1987). Studies elucidating a possible genetic basis for differential migration behavior (see e.g. Hess et al. 2016) would be an important future direction to pursue, but such an analysis was beyond the scope of the present study.

4.2. Irregularities in migration patterns

Some otoliths in the present study showed high Sr:Ca ratios, above the defined threshold separating the low- and high-salinity regime, in the innermost (i.e. earliest observed) measurements (Fig. S1, Nos. 2, 7 and 10). The lack of information for the earliest life stage provided by the Sr:Ca signal profile (the first 150 µm were removed from each profile) combined with the tendency of a relatively fast downstream migration as observed for stocked juvenile fish of 20–60 mm TL in the Rhine system (Borcherding et al. 2006) could be a significant factor in this observation. Since there is no evidence that reproduction of *C. maraena* can occur in high-salinity habitats in the North Sea, it can be assumed that these individuals also initially lived in the low-salinity regime. According to Jensen et al. (2003), the physiology of maraena whitefish changes when an individual reaches a total length of 30–40 mm, so it can withstand the move to high-salinity waters from that point on.

In contrast, 2 other otoliths showed high Sr:Ca ratios at the end of the profiles (Fig. S1, Nos. 8 and 9). A straightforward reason here may be that these individuals had only recently migrated into the River Elbe, where they were captured and had not spent enough time in low-salinity waters for this to be reflected in the otoliths as correspondingly low Sr:Ca ratios. Such a time-delayed response of otolith Sr:Ca ratios to Sr variation in the ambient water has been noted in previous studies (e.g. Yokouchi et al. 2011). The time required to establish the state of equilibrium between Sr content of the otoliths and the surrounding water may not have been reached in these cases. According to Elsdon & Gillanders (2005), it may take 20 d before an Sr signal, corresponding to a new environment, is fully reflected in otoliths. This time-delayed response may also have biased the data points of reference fish used to validate the differentiation among salinity regimes. Ideally, all reference fish should have originated from salinities under controlled conditions. However, these fish were not available, and results of the multimodal frequency distribution as well as similar findings of Rohtla et al. (2017) suggest that the use of the last 6 data points worked quite well.

The unexpected positive correlation between Sr:Ca and Ba:Ca ratios in resident individuals may be explained by the small range of Sr:Ca ratios close to the lower bound of measured ratios (0.13–2.09 mmol mol^{-1}) compared to the range found in migratory individuals (0.34–11.04 mmol mol^{-1}), which could prevent the identification of a negative correlation. Furthermore, slight variations in the Sr:Ca ratios within the low-salinity regime probably indicate small-scale migrations within the river system, changes in water temperature, food availability or age-related changes in storage rates (Campana 1999, Secor & Rooker 2000), which alter the uptake and incorporation of Sr into fish otoliths (Sadovy & Severin 1992, Bath et al. 2000). However, these effects are weaker than the effects of water salinity on Sr incorporation into otoliths (Marohn et al. 2009, 2011) and are thus expected to be of minor importance. The salinity in the Elbe estuary changes over the tidal cycle, as tidal currents move a water body between 15 and 20 km down- and upstream twice a day (Bergemann 1995). This could cause slight variations in salinity at sampling locations and it cannot be ruled out that these variations are also reflected in otolith elemental composition to a minor extent.

Ba:Ca ratios varied strongly within the measured profiles of resident individuals. Ba uptake into otoliths is mainly driven by its availability in surrounding water (Hüssy et al. 2020) but can also be affected by other environmental factors. Bath et al. (2000) found that e.g. temperature can significantly influence the Sr:Ca ratio of marine fish but has no effect on the incorporation of Ba into the otoliths. However, other studies reported significant temperature effects on Ba incorporation into otoliths, e.g. for black bream *Acanthopagrus butcheri* (Elsdon & Gillanders 2002) and European eel *Anguilla anguilla* (Marohn et al. 2011), suggesting species-specific dif-

ferences of temperature effects on the incorporation of Ba into otoliths. To determine if and to what extent temperature or other potential factors (e.g. growth; Walther et al. 2010) are responsible for the observed Ba fluctuations is notoriously complex and beyond the scope of this study.

4.3. Migratory behavior in relation to sex

The lack of differences in migration behavior between sexes in our study contrasted with strong differences observed in many other partially migratory salmonid fish species (Jonsson & Jonsson 1993, Chapman et al. 2012a, Dodson et al. 2013). Among salmonids, females typically dominate the migratory contingent, e.g. in brown trout *Salmo trutta* and Atlantic salmon *S. salar* (Jonsson & Jonsson 1993, Klemetsen et al. 2003). A reason for female-biased migration may lie in the strong correlation of fecundity and body size; migrating to the highly productive marine environment may increase reproductive success through better growth to a greater extent for females than for males (Gross 1987, Jonsson & Jonsson 1993, Klemetsen et al. 2003). The similar observations for males and females in our study would be in line with the observed high proportion of permanent residency that pointed to sufficient feeding conditions within the Elbe.

4.4. Migratory behavior in relation to fish size

Body size may be an important trait that could have an impact on whether to migrate or not (Chapman et al. 2012a, Dodson et al. 2013). Although information on body size before the time of first migration to a high-salinity regime was not available in the present study, body size of older individuals indicated that migrants were larger than residents, with significant differences in AG 2 and the same trend (but without significant differences) in AG 3. This is consistent with previous observations for different species including coregonids (Mehner & Kasprzak 2011; reviews by Chapman et al. 2012a and Dodson et al. 2013). In temperate waters, the sea generally offers richer feeding grounds than the freshwater environment. This allows migrants to have a higher growth rate compared to resident individuals, which results in larger body size at the same age (Gross 1987, Jonsson & Jonsson 1993). Factors such as low population density and good feeding opportunities in the freshwater system that favor residency over migratory behavior (Jonsson & Jonsson 1993) could also have led to the less pronounced differences in body size between migrants and residents of *C. maraena* in the Elbe.

4.5. Implication for conservation measures

The survival of endangered species directly depends on the availability of suitable habitat (Cooke et al. 2012, Arthington et al. 2016). Understanding habitat needs of such species is therefore critical information to support conservation efforts.

A complex stock structure, which is characterized by both residency and migration behavior, emphasizes the need for a differentiated approach to species-specific needs. Resident individuals do not only use the habitat for spawning but also as a feeding habitat throughout the year. The entire life cycle takes place in a relatively small geographical area, which is therefore of crucial importance for the survival of these individuals. Migratory individuals, on the other hand, also need marine habitats and rely in particular on open migration routes to switch between habitats to complete their life cycle. Consequently, the present study identifies the River Elbe system as a crucial area that is used year-round by an important proportion of the population, and is thus relevant as a feeding, spawning and wintering habitat as well as a migration route for maraena whitefish. From this, a need for year-round protection of the riverine habitat can be derived.

However, the Elbe is exposed to strong human impacts such as canalization, industry and fisheries (Kammerad 2001b, Thiel 2011). Commercial shipping in particular is of great importance (Boehlich & Strotmann 2008). In this context, deepening of the navigation channel has considerably altered the river, which has not only affected the tidal dynamics of the river, but also its biota, including fishes (Thiel 2011). Further investigations of the species-specific habitat use within the Elbe and the impacts of anthropogenic activities on the quality of these habitats would thus have strong potential to support effective management strategies and improve the protection of this priority fish species in the context of the Habitats Directive.

4.6. Conclusions

The partial migration within the *C. maraena* population in the Elbe estuary observed here represents an example of phenotypic plasticity in a fish that pos-

sibly increases fitness under variable environmental conditions (Jonsson & Jonsson 1993). The occurrence of migrations between the River Elbe and the Wadden Sea, but also a substantial proportion of permanent or at least long-term freshwater habitat use, provides new knowledge to inform conservation decisions. Specifically, it highlights the importance of the Elbe as both feeding and spawning habitat, but also the importance of maintaining migration corridors and connectivity within the system.

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